

of observation. It appears also that continuous stimulation of the insects through HFS does not bring about, at least at the frequency tested, any accumulation of the effect. It cannot be excluded, however, that HFS may induce other modifications that are not recorded by this method.

This technique can, therefore, be employed for studying the motor activity of male *P. americana* under different conditions.

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Some Factors Affecting Oviposition Behavior of the Mountain Pine Beetle^{1,2}

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ABSTRACT

Four factors that affect oviposition behavior of *Dendroctonus ponderosae* Hopkins in lodgepole pine, *Pinus contorta* Douglas, were investigated. These were distance between egg galleries, size of the female, phloem thickness, and temperature.

The average number of eggs oviposited per inch of gallery increased with increases in each of the 4 factors. The average number of eggs oviposited per day also increased with increases in each factor except that the effect of distance between galleries was not investigated. The rate of gallery construction increased only with an increase in temperature; it was unaffected by size of female and phloem thickness. Again the effect of distance between galleries was not investigated.

Knowledge of oviposition behavior has become increasingly important in understanding the dynamics of populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in lodgepole pine, *Pinus contorta* Douglas. The oviposition of too many eggs could result in intraspecific competition among developing larvae and bring about reduced survival as observed by Cole (1962). On the other hand, the oviposition of too few eggs could result in less brood production than potentially possible from phloem of a given thickness (Amman 1972).

Reid (1962) found that large mountain pine beetles generally laid more eggs than did small beetles in lodgepole pine. He also observed that more than 200 eggs were deposited in some individual galleries that were more than 50 in. long, when phloem remained moist and temperatures were

above ca. 7.2°C. In terms of overall response, Reid found an average of 4.2 eggs/inch. This average is similar to some found by Cole³ in 3 infested areas: 4.26/inch of gallery in Utah; 4.78 in Wyoming; and 5.85 in Idaho.

Laboratory studies reported here were conducted to determine the effects on oviposition behavior of: (1) spacing between egg galleries; (2) beetle size; (3) phloem thickness; and (4) temperature.

Methods

Effect of Gallery Spacing

Billets 14 in. long were cut from a single tree in which thickness of phloem exceeded 0.10 in. From the billets, 12 slabs 6×14 in. and ca. 2 in. thick were

¹ Coleoptera: Scolytidae.

² Received for publication 25 Feb., 1972.

³ W. E. Cole. The mountain pine beetle in lodgepole pine, *Dendroctonus monticolae* Hopk. (Coleoptera: Scolytidae). Studies of populations. Progress Report—Study II. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah. Mimeogr., 20 p. 1964.

cut. All exposed wood and the edges of the bark of material used in these studies were waxed to prevent rapid loss of moisture. Beetles (without regard to size) were introduced into holes in the bases of 3 slabs for each of 4 rates—3, 6, 9, and 12 pairs. The 4 rates were used so that a large range in gallery spacing would result. The slabs were stored at 21.1°C for 10 days. The bark then was peeled and the eggs deposited on left and right sides of the gallery were counted in each inch. Distance between paired inches of egg galleries was recorded.

Effect of Beetle Size

Billets 14 in. long were cut from a single tree that had an average phloem thickness of 0.17 in. Seventy-two pairs of beetles (females 4.3–6.4 mm long) were introduced at 2-in. intervals around the circumference of the bases of the billets; the billets were stored at 21.1°C for 12 days. The bark then was peeled and the eggs in each inch of gallery were counted.

Effect of Phloem Thickness

Billets 14 in. long were cut from 4 lodgepole pines, all growing within a 1/2-acre area. Each tree had a different average phloem thickness: 0.06 in., 0.10 in., 0.15 in., and 0.19 in. Twenty pairs of beetles (females 4.3–6.4 mm long) were introduced at 2-in. intervals around the circumference of the bases of the billets. Care was taken to assure that an equal number of females of each size was placed in billets representing each of the 4 trees. The infested billets were stored at 21.1°C for 11 days. The bark then was removed and the eggs in each inch of gallery were counted. At this time thickness of phloem and depth at which beetles excavated the sapwood (2 in.) above the beginning of each egg gallery were measured.

Effect of Temperature

Four billets 14 in. long were cut from a single tree. Phloem thickness in these billets ranged from 0.12 to 0.15 in. Twenty pairs of beetles (females 4.3–5.5 mm long) were introduced at 2-in. intervals around the circumference of the bases of the billets. The 4 billets were stored at room temperature (22°C) for 1 day to allow the beetles time to initiate egg galleries and to mate, and then each was stored an additional 13 days at a different temperature—7, 10, 15, or 20°C. The bark then was removed and the eggs were counted.

Results

Effect of Gallery Spacing

The average number of eggs laid on sides of adjacent galleries ranged from 1.7/inch for galleries spaced 1/2 in. apart to 3.6/inch for galleries spaced 3/8 in. apart. The curve is almost asymptotic where galleries are 1 in. apart; therefore, the activities of adjacent beetles probably would have little effect at distances greater than 1 in.

However, the low correlation coefficient for individual observations ($r^2=0.023$; $n=395$) and large

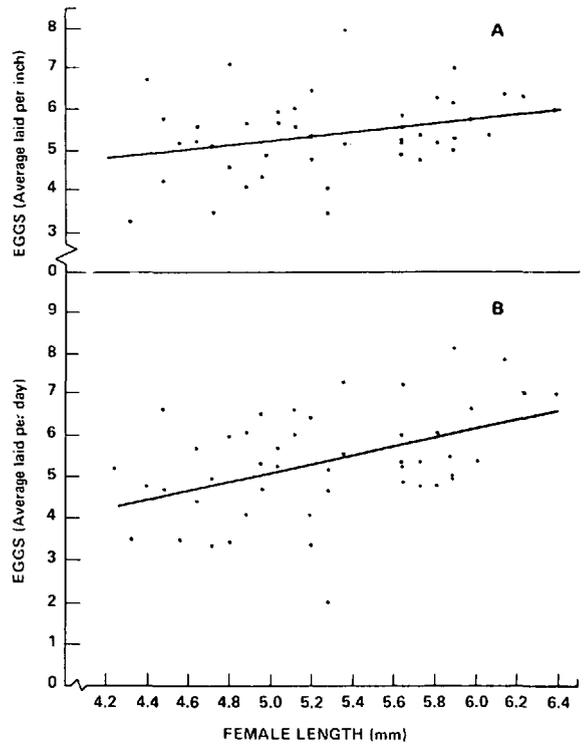


FIG. 1.—The relation of oviposition behavior to length of female mountain pine beetle.

A. The average number of eggs laid per inch (2.54 cm) of gallery.

$$\hat{Y} = 2.52 + 0.54X; S_{Y.X} = 0.91; r^2 = 0.09; F < 0.05$$

B. The average number of eggs laid per day.

$$\hat{Y} = -0.261 + 1.06X; S_{Y.X} = 1.17; r^2 = 0.20; F < 0.005$$

standard deviation ($S_{Y.X}=2.07$) indicate that the main sources of variance were not identified. A possible source of variance is that not all beetles bored at the same rate. When beetles bore at the same rate, one beetle might detect sounds of current gallery constructing activities of an adjacent beetle and reduce oviposition. However, where one beetle bored ahead of its neighbor, previous gallery construction might be sensed and oviposition reduced only because of drying of phloem and the action of fungi, bacteria, and yeasts.

Effect of Beetle Size

The average number of eggs laid per inch of gallery ranged from 3.2 for a beetle 4.3 mm long to 7.9 for a beetle 5.4 mm long (Fig. 1A). The relation, although significant ($P < 0.05$), was weak and accounted for only 9% of the variance.

The average number of eggs laid per day ranged from 3.4 for a beetle 4.3 mm long to 8.2 for a beetle 5.9 mm long (Fig. 1B). This relation also was weak, accounting for only 20% of the variance. Consequently, tremendous variation in egg-laying capacity existed among beetles of a similar size, even when held under similar conditions of food, temperature, and egg-laying substrate. However, there was no clearcut indication that oviposition declined

in the largest beetles, which corroborated observations by Reid (1962).

The average length of gallery constructed per day was not significantly related to beetle length ($P > 0.05$).

Effect of Phloem Thickness

The average number of eggs laid ranged from 3.5/ inch in phloem 0.06 in. thick to 9.6 in phloem 0.18 in. thick. Although this relation was significant ($P < 0.01$), it accounted for only 16% of the variance (Fig. 2A).

The average number of eggs laid per day ranged from 1.7 in phloem 0.06 in. thick to 7.7 in phloem 0.20 in. thick. Although this relation also was significant ($P < 0.025$) it only accounted for 14% of the variance in rate of oviposition (Fig. 2B).

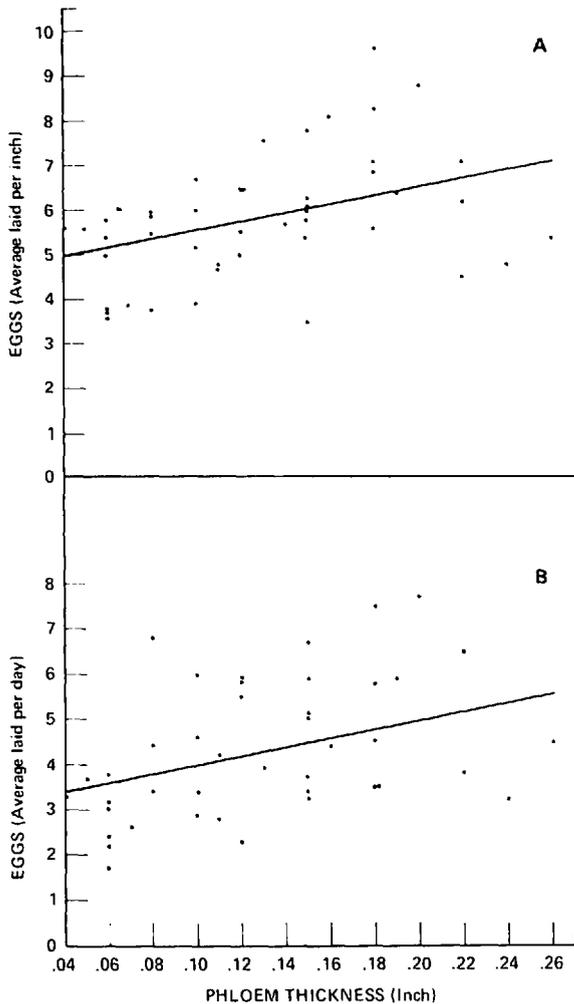


FIG. 2.—The relation of oviposition behavior of the mountain pine beetle to thickness of lodgepole pine phloem.

- A. The average number of eggs laid per inch (2.54 cm) of gallery.
 $\hat{Y} = 4.51 + 0.91X$; $S_{y \cdot x} = 1.3$; $r^2 = 0.16$; $P < 0.01$
- B. The average number of eggs laid per day.
 $\hat{Y} = 3.02 + 0.65X$; $S_{y \cdot x} = 1.39$; $r^2 = 0.14$; $P < 0.025$

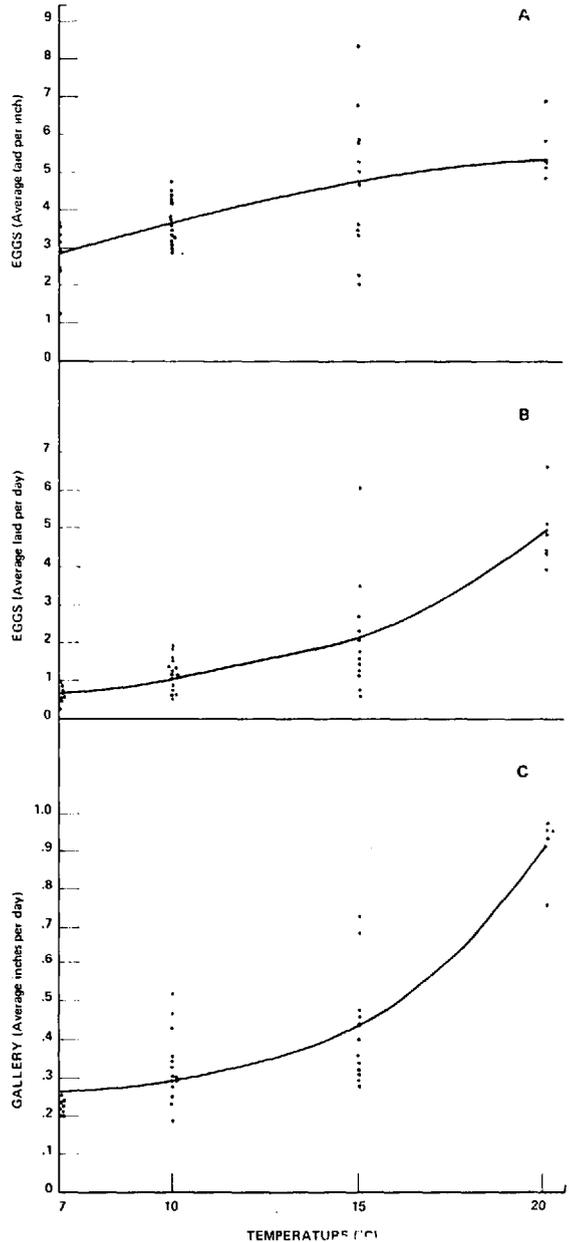


FIG. 3.—The relation of oviposition behavior of the mountain pine beetle to temperature.

- A. The average number of eggs laid per inch (2.54 cm) of gallery.
 $\hat{Y} = 5.32 - 0.0547(20-X)^{1.49}$; $S_{y \cdot x} = 1.16$; $r^2 = 0.35$; $P < 0.005$
- B. The average number of eggs laid per day.
 $\hat{Y} = 0.146 + 0.96 \cdot 0.75 + 0.01293(X-7)^{2.25}$; $S_{y \cdot x} = 0.91$;
 $r^2 = 0.70$; $P < 0.005$
- C. The average length of gallery constructed per day.
 $\hat{Y} = 0.014 + 0.986 \cdot 0.274 + 0.00023(X-7)^{3.105}$; $S_{y \cdot x} = 0.11$;
 $r^2 = 0.81$; $P < 0.005$

The relation between rate of gallery construction and phloem thickness was not significant. This was surprising because beetles that constructed galleries in thin phloem excavated deeper into the sapwood

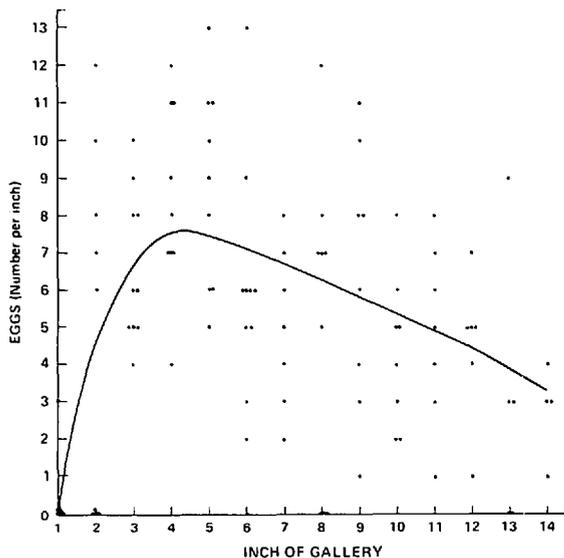


FIG. 4.—Numbers of eggs laid per inch (2.54 cm) of gallery (46 galleries 6–14 in. long) ($\frac{1}{2}$ of data plotted).

$$\hat{Y} = 7.65 - \left[A \left(\frac{1}{2} + \frac{1}{2} \left[\frac{4.25 - X}{4.25 - X_1} \right] \right) + B \left(\frac{1}{2} + \frac{1}{2} \left[\frac{X - 4.25}{X - 4.35} \right] \right) \right]$$

$$A = 7.35 \left[\frac{4.25 - X}{(5.25)^{2.09}} \right]$$

$$B = 4.50 \left[\frac{X - 4.25}{(9.75)^{1.215}} \right]$$

$$1 \leq X \leq 14 \text{ and } X \neq 4.25$$

$$S_{Y \cdot X} = 2.71; r^2 = 0.54, P < 0.005$$

than did those in thick phloem. Averages ranged from 0.045 in. of sapwood excavation where phloem was 0.04 in. thick to 0.01 in. of excavation where phloem was thicker than 0.12 in. ($r^2=0.55$; $P < 0.005$; $S_{Y \cdot X}=0.012$). Furthermore, the wood was harder than bark; consequently, more time should have been required to excavate wood than bark.

A possible explanation for differences in rates of oviposition and numbers of eggs laid in thin and thick phloem might be related to nutrition; the thin phloem and the excavated xylem might provide less energy than thick phloem. Another possible explanation is that beetles expended more energy in constructing egg galleries where the xylem was excavated, which left less energy for egg production than would occur during gallery construction in thick phloem.

Effect of Temperature

The average number of eggs laid per inch of gallery ranged from 1.3 at 7°C to 8.3 at 15°C. However, this accounted for only 35% of the variance (Fig. 3A).

The number of eggs laid per day ranged from an average of 0.23 at 7°C to 6.6 at 20°C (Fig. 3B). Rate of oviposition remained low even at 15°C; however, it increased rapidly at 20°C. This relation is strong; it accounted for 70% of the variance.

Gallery construction ranged from an average of

0.20 in./day at 7°C to 0.98 in./day at 20°C (Fig. 3C). Again, a curvilinear relation is indicated; a big increase occurred at 20°C. This relation also is strong, accounting for 81% of the variance.

Note in Fig. 3A that the curve almost peaks at 20°C. Consequently the number of eggs deposited at higher temperatures would not be expected to increase much. However, the curves in Fig. 3B and 3C continue to rise at 20°C; therefore, both the length of gallery constructed per day and the number of eggs deposited per day could be expected to peak at temperatures higher than 20°C.

Overall Response

The overall ovipositional response in each inch of gallery was based on 46 galleries that were 6–14 in. long; these were constructed during the study of the effect of gallery spacing. From the regression line in Fig. 4, the average number of eggs laid per inch ranged from 0.28 in the 1st inch to 7.7 in the 4th inch; oviposition peaked in the 4th inch of the smoothed curve. The average number of eggs laid in the 1st inch was only 0.28; the overall average was 5.43.

Cole³ observed from field measurements in 3 locations that oviposition ranged from 0.25 to ca. 11 eggs/inch; oviposition peaked either in the 2nd or 3rd inch of gallery. He reported that average number of eggs deposited in the 1st inch of gallery ranged from 0.25 to over 10; the overall averages for the 3 locations ranged from 4.26 to 5.85 eggs/inch.

The overall average observed in the laboratory was within the range of averages observed by Cole, indicating that the response of beetles probably was similar in the 2 situations. However, considerable difference was noted in numbers of eggs laid in the 1st inch of gallery. The larger number laid in the 1st inch in the field may account for the fact that oviposition peaked earlier in the gallery in the field than it did in the laboratory.

Two factors that may be involved in oviposition differences between the laboratory and the field are (1) physiological changes and (2) time of fertilization. Reid (1958) and McCambridge and Mata (1969) noted that the newly attacking female did not oviposit until the flight muscles had degenerated greatly (degeneration usually occurred within 3 days).

Time of fertilization in the field could differ considerably. For example, fertilized females making a 2nd gallery would probably start laying eggs almost immediately, whereas unfertilized females making their 1st gallery may have to wait one or more days before a male arrived, especially when the females greatly outnumber the males. In the laboratory, the female was allowed one day to construct a gallery before the male was introduced.

Discussion

As infestations of the mountain pine beetle progress, the beetles infest smaller trees because many of the larger trees are killed during the early years

of the infestation (Cole and Amman 1969). The small trees usually have thin phloem, and fewer beetles per ft² of bark attack them than attack large trees.⁴ In addition, beetles that complete development in small trees are smaller than those that complete development in large trees (Safranyik and Jahren 1970). As a result of the phloem being thinner and beetles being smaller, we would expect fewer eggs to be laid; the low amount of oviposition and low density of attacking beetles would reduce competition among developing larvae. However, possible built-in mechanisms that tend to reduce intraspecific competition are not so effective that the beetle can maintain or increase its numbers in small trees that have thin phloem.

The effect of temperature on oviposition might explain partially the lower emergence of brood adults from bark of a given thickness at high elevations in contrast to low elevations as observed by Amman (1969). Reduced oviposition could result in fewer brood adults being produced than is potentially possible for phloem of any given thickness. The low number of beetles emerging per ft² of bark has resulted in fewer trees being killed at high elevations than at low elevations (Amman and Baker 1972).

Acknowledgment

The algebraic descriptions of curves by Chester E. Jensen and Jack W. Homeyer, Statisticians, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, are gratefully acknowledged.

⁴ Unpublished data. Project 2201, Intermountain Forest and Range Experiment Station, Ogden, Utah.

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Spatial Distribution Patterns of *Lygus* Bugs¹ in California Cotton Fields²

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ABSTRACT

Adults and nymphs of *Lygus hesperus* Knight and *L. elisus* Van Duzee were found to be distributed in cotton fields in clumped, nonrandom patterns. The nymphs showed more clustering than the adults. The adults and nymphs were consistent in their degree of clumping between 8 AM and 6 PM. The observed distribution patterns were fitted by several contagious mathematical models. Statistical analyses indicate the feasibility of using theoretical distributions to describe samples based on adult-plus-nymph or adult-plus-twice-nymphs counts.

A primary requisite to better understand an organism in its ecosystem is knowledge of its spatial distribution (= dispersion) patterns. These patterns are manifestations of the inherent biological charac-

teristics of the species as influenced by the environmental factors in a given habitat, and, as such, reflect the influence of these factors on the organism's mode of life.

Correct experimental design and effective sampling methods cannot be devised until the distribution pattern is known. Thus, demographic studies cannot be properly conducted on population den-

¹ Hemiptera: Miridae.

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